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Markov simulation model: Flooding, competition, and the fate of the endemic plant *Myosotis rehsteineri*

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Running title: Dynamics of Myosotis rehsteineri under flooding

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Abstract

By Markov simulation modelling we analyzed an almost continuous monitoring series over 27 years of the abundance of the highly endangered amphibious plant species *Myosotis rehsteineri* at the shore of Lake Constance (Germany). The habitat is characterized by yearly floodings of variable magnitude that produce a zonation of species with different flood tolerance. A transect was established in 1983, perpendicular to the shoreline, and divided into segments (2 x 2m) of different flood duration. Population sizes, expressed as the number of inflorescences, were determined per segment and year. Additionally, we had detailed data on flooding and knowledge on the dynamics of competing species. A Markov model fitted by nonlinear least squares against the time series of spatially structured abundance data proved to be a useful tool to evaluate population dynamics and to assess the effects of varying environmental conditions that are not accessible to experimental control. Water-level fluctuations and competition by *Agrostis stolonifera* were both found to affect the population dynamics of *M. rehsteineri,* but without causing a long-term change in population size under present conditions. The modelling enabled us to evaluate different flooding scenarios and thus providing support for future conservation measures, and we found that extinction risk will increase under changing flooding regimes. Our data and the results of the Markov model simulations showed that under strong abundance fluctuations long-term monitoring is indispensable to explore population dynamics of rare and endangered species in their natural context.

Zusammenfassung

Auf der Basis eines Markov-Simulationsmodells analysierten wir eine 27 Jahre währende, fast ununterbrochene Beobachtungsreihe der Häufigkeiten der stark gefährdeten amphibischen Pflanzenart *Myosotis rehsteineri* am Bodenseeufer (Deutschland). Das Habitat dieser Art ist charakterisiert durch jährliche, in der Höhe schwankende Überschwemmungen, welche eine Zonierung von Pflanzenarten unterschiedlicher Hochwassertoleranz bewirken. Im Jahre 1983 wurde ein Transekt senkrecht zur Uferlinie eingerichtet, welches in Segmente von 2 x 2 m unterteilt wurde. Bis 2009 wurden nahezu in jedem Jahr in jedem Segment die Populationsgrößen durch Bestimmung der Zahl der Infloreszenzen ermittelt, außerdem Details des Hochwasserverlaufs und der Dynamik konkurrierender Arten. Wir zeigen, dass Markov-Modelle, deren Parameter durch nichtlineare Regression anhand der Abundanz-Zeitreihen geschätzt wurden, ein nützliches Instrument zur Analyse solcher Einflußfaktoren darstellen, die im Experiment nicht kontrolliert werden können. Für *M. rehsteineri* ergab die Analyse, dass Wasserstandsfluktuationen und konkurrierende Arten wichtige Einflussgrößen darstellen, welche die Populationsentwicklung begrenzen ohne jedoch einen langfristigen Trend in der Populationsgröße unter gegenwärtigen Bedingungen zu verursachen. Die Modellierung erlaubt es, mögliche Veränderungen im Hochwasserregime in ihren Auswirkungen zu testen, und es wurde festgestellt, dass Änderungen im Hochwasserregime sich negativ auf die Überlebenschancen von *Myosotis* auswirken. Unserer Analyse und Markov-Modellsimulationen zeigten, dass bei starken Häufigkeitsschwankungen Langfristbeobachtungen unerlässlich sind, um zuverlässige Aussagen zur Populationsdynamik seltener und gefährdeter Arten in ihrem natürlichen Zusammenhang zu erhalten.

Keywords: amphibious plant; extinction risk; lakeshore; Lake Constance; long-term study; monitoring; space-time modelling; water-level fluctuations

66 **Introduction**

67

68 *Myosotis rehsteineri* is a narrow-range endemic plant species almost exclusively occurring at
69 exposed gravel lakeshores of the pre-Alpine Lake Constance (Germany, Switzerland, and
70 Austria). The small perennial plants occur on nutrient poor sediments, which are flooded each
71 year for 2-6 months. The species is highly endangered (Dienst, Strang & Peintinger, 2004) and
72 protected by the EU habitat directive 92/43/EEC. In the course of the 20th century many
73 populations of *Myosotis rehsteineri* were destroyed, mainly by habitat destruction (Dienst et al.
74 2004). Increasing nutrients loads (eutrophication) led to a spread of competitors and to the
75 deposition of algal washes, which both decreased the viability of *M. rehsteineri* as a weak
76 competitor (Thomas, Dienst, Peintinger & Buchwald, 1987). However, due to the building of
77 water purification plants a phase of re-oligotrophication of Lake Constance has begun (Sommer,
78 Gaedke & Schweizer 1993; IGKB 2004), and also the amount of algal deposits has declined
79 (Schmieder & Pier 2000). However, the remaining populations of *Myosotis rehsteineri* are often
80 small and isolated (Dienst et al. 2004). Some evidence was found that the population dynamics of
81 *M. rehsteineri* is influenced by inter-annual variation in flood duration and that the fate of
82 populations will be affected by long-term trends in flood duration (Peintinger, Strang, Dienst &
83 Meyer 1997; Peintinger 2007).
84 In 1983 a monitoring was started by establishing a permanent transect to estimate abundance
85 dynamics of *Myosotis rehsteineri*. Competing species were not directly studied but there is
86 detailed knowledge about spread and flood dependence of all relevant species of the community
87 from similar investigations at other sites of Lake Constance (Peintinger, Prati & Winkler 2007).
88 A model analysis of spatially structured abundance data that explicitly includes the effect of
89 external biotic and abiotic factors allows for predicting species development when such factors

90 are changing. Such a strategy, based on Markov simulation models, was followed by Peintinger
91 et al. (2007) for a series of species characteristic for the same lakeshore community at Lake
92 Constance. Our present analysis of *Myosotis rehsteineri* dynamics aimed at answering the
93 following questions:
94 1) Can population dynamics of *Myosotis rehsteineri* observed for the time period 1983-2009 be
95 explained as a function of flood duration and the impact of a competitor?
96 2) What is the long-term trend in species abundance and in competitor development?
97 3) What are the consequences of changes in average flood duration on the persistence of *Myosotis*
98 *rehsteineri* populations?
99
100 **Materials and methods**
101
102 *Study system*
103
104 The exposed parts of the shores of Lake Constance contain an amphibious plant community,
105 which is phytosociologically described as *Deschampsietum rhenanae* (Lang, 1973). The
106 community consists of amphibious plant species (< 10 cm height). Vegetation cover is low and is
107 decreasing toward the lakeside of the shore. *Myosotis rehsteineri* (Boraginaceae) is endemic to
108 pre-Alpine lakes. Reproduction occurs sexually and by clonal growth (Peintinger 2007). It is
109 flowering early in spring before water level rises. If the water levels increases early in the spring
110 seed formation fails completely. During flowering *M. rehsteineri* forms (aboveground) stolons,
111 which decay rapidly resulting in physiologically independent daughter rosettes.
112 The water level of Lake Constance usually reaches a maximum in June-July due to the increase
113 in precipitation and snowmelt. The mean amplitude of water-level fluctuations is nearly 2 m

(Jöhnk, Straile & Ostendorp, 2004). The study period was characterized by two extremes. In 1999 the highest water level since 1890 was observed (Jöhnk et al. 2004), followed by a period of high flood levels until 2002. Extremely dry summer in 2003 led to the lowest summer water level ever measured at Lake Constance (Ostendorp, Brem, Dienst, Jöhnk, Mainberger et al. 2007); other low flood levels were founds in several years after 1990 (Fig. 1A). Average flood duration decreased between 1960 and 2009, but slope of linear regression (b = -0.042 $\pm$ 0.030) was not significantly different from zero (Fig. 1A). Using a longer time series, Jöhnk et al. (2004) have found a decline of water level since 1925.

Field study

Our study was conducted near the village Hegne at the Lake Constance ("Untersee") in Southwest Germany (Baden-Württemberg; N 47°42'15''/E 9°05'42''). Here *Myosotis rehsteineri* is growing together with *Ranunculus reptans*, *Littorella uniflora,* and *Agrostis stolonifera* (for phytosociological relevés see Appendix A: Table 1). In 1983 a permanent transect was established, covering the lakeshore vegetation. The transect was arranged perpendicular to the shoreline and marked with iron tubes. It had a size of 2 m x 28 m, divided into 14 segments of 2 x 2 m size. Between 1983 and 2009 we estimated population size by counting the numbers of inflorescences in each segment in April or May. Data are completely missing in 7 of the 27 study years. In three further years (1996, 1999, 2000) only the total number of rosettes could be counted. The number of flowering rosettes for those years were estimated assuming that about 2/3 of all rosettes are flowering (M. Dienst, unpubl. data).

The counting of the number of inflorescences per segment i and year t gave abundance values $a_i(t)$. Relative change in abundance was defined as

$$R_i(t) = \ln[(a_i(t)+1)/(a_i(t\text{-}1)+1)], \quad (1)$$

except in cases when either $a_i(t)$ or $a_i(t\text{-}1)$ were missing.

The elevation of the segments relative to the water gauge of Constance (zero point: 391.89 m a.s.l., Jöhnk et al. 2004) was measured using a standard levelling device (Fig. 1B). To determine the course of flooding over the transect we started from the set of annual flood duration values τ_0, expressed in time units τ of 15 days, at the level of 340 cm as given above (Fig. 1A). The time step size of 15 days averaged out some unevenness of the relief. Following Peintinger et al. (2007) who considered an average change in flood duration of 0.76 time units (approx. 11.4 days) per 10 cm level difference we calculated flood duration per segment for each year (Fig. 1B).

Markov model of species abundances

We developed Markov models to analyse the time dependence of *Myosotis rehsteineri* abundance and of the cover of the competing grass *Agrostis stolonifera* (hereafter we used only the genus name) in the m segments of the transect (m = 14). The Markov models consisted of a set of stages, the segments of the transect, with a vector **a** representing the state variables of the system (abundance values $a_i(t)$ for *Myosotis* or frequency values $f_i(t)$ for *Agrostis*, with segment index i = 1,…,14), and of a matrix **C** containing the rates of stage transitions that were depending on flooding with annually varying duration τ_i. Both species models were linked by the assumption that *Agrostis* frequencies were influencing the transition rates for *Myosotis*. For *Myosotis* we introduced:

$$\mathbf{a}(t+1) = \mathbf{C}\ \mathbf{a}(t) \quad (2)$$

with state vector **a**:

161 $$\mathbf{a} = \begin{pmatrix} a_1 \\ a_2 \\ \vdots \\ a_m \end{pmatrix} \quad (3)$$

162 and the initial conditions for the segments

163 $$a_i(t = 0) = a_i(0) \quad (4)$$

164 Abundances were limited by

165 $$0 \leq a_i(t) \quad (5)$$

166 The transition matrix **C** was constructed as

167 $$\mathbf{C} = \left(\begin{array}{ccc:cc} A_1 B^{\tau_1} - D - (m-1)d & D + d & d & d & d \\ D + d & A_2 B^{\tau_2} - 2D - (m-1)d & D + d & d & d \\ \hdashline d & d & d & D + d & A_m B^{\tau_m} - D - (m-1)d \end{array}\right) \quad (6)$$

168 where A and B are year-to-year transition parameters for each segment, and D and d are dispersal

169 constants (see below).

170 The flood-independent rate components A_i in the matrix (eq. 6) contained a segment-independent

171 parameter A and depended on the frequency f_i of *Agrostis* in the same segment i:

172 $$A_i = A\,(1 - \gamma\, f_i), \quad (7)$$

173 with γ a one-sided competition constant. The power expression $B^{\tau i}$ describes flood-dependence of

174 transition. Flood duration τ_i per segment i was computed as described above. For $\tau_i \geq 12$ at time t

175 the abundance a_i for segment i at t+1was set to zero:

176 $$a_i(t+1) = 0 \text{ if } \tau_i(t) \geq 12. \quad (8)$$

177 Thus, flood durations of 6 months or more will act as a local "catastrophe", in accordance with

178 the high mortality rates observed after extremely long flooding (Peintinger, 2007).

179 The dispersal constant D described spread into adjacent segments within the transect and

180 corresponded to short-distance seed dispersal and clonal growth, whereas d described general

181 dispersal from one segment to each of the (m-1) other segments, corresponding to dispersal by
182 seeds.
183
184 Dynamics of *Agrostis* were described in a similar way, but with "frequencies" f_i as state
185 variables: the state of *Agrostis* in a segment was characterized by counting the numbers of sub-
186 segments (squares of 10 cm x 10 cm) occupied by the species (see Peintinger et al., 2007).
187 Therefore frequency values were limited by
188 $$0 \le f_i(t) \le 1. \qquad (9)$$
189 For *Agrostis* only local spread (parameter D_{AS}) was detectable (Peintinger et al., 2007).
190 Immigration from the landside was irrelevant as in the landside segments the upper limit of eq. 9
191 was always reached. The transition matrix for *Agrostis* thus reads as:
192 $$C_{AS} = \left(\begin{array}{ccc:cc} A_{AS}B_{AS}^{\tau_1} - D_{AS} & D_{AS} & 0 & 0 & 0 \\ D_{AS} & A_{AS}B_{AS}^{\tau_2} - 2D_{AS} & D_{AS} & 0 & 0 \\ \hdashline 0 & 0 & 0 & D_{AS} & A_{AS}B_{AS}^{\tau_m} - D_{AS} \end{array}\right) \qquad (10)$$
193 For *Agrostis* intra-specific density regulation could be neglected (Peintinger et al., 2007), and we
194 assume that the plants were not affected by the weak competitor *Myosotis*. Hence, the rate
195 component A_{AS} was independent of segment position.
196 Model parameters in the Markov model eq. 6 (A, B, D, and d) were estimated by nonlinear
197 regression analysis based on the abundance records 1983 to 2009 and on flood duration values in
198 the period 1983-2008 (for details see Appendix A).
199
200 *Projection scenarios*
201

We used the parameter estimates for projecting population development of *Myosotis*. Simulations started in 1983, and the projection period ended in 2057, i.e. 75 years after start of the study. For each year after 2008, a basic value τ_0 for flood duration was drawn at random from the set of values given in Fig. 1A. To study the effect of changes in average flood duration, a value $\Delta\tau$ ($\Delta\tau = -2$ or $+2$) was added to each $\tau_i(t)$. Additionally, the $\Delta\tau = -2$ scenario was modified by the assumption that the longest τ-period ($\tau = 14$) remained unchanged. As the Markov model gave real numbers for the state variables, *Myosotis* was denoted as extinct, if $a_i < 1$ in all segments i. For each scenario 1,000 runs were performed, giving average final species distribution over the segments and extinction probability p_{ext} for *Myosotis*.

Results

Time-series analysis: Dynamics of Myosotis *in the study transect*

The field data are compared with simulated *Myosotis* abundances that gave best approximation to the field data of *Myosotis*, combined with simulated *Agrostis* frequencies (Fig. 2). The fit of *Myosotis* abundance data gave the parameters of Table 1, together with the dispersal parameter D_{AS} for *Agrostis* that was determined indirectly from the *Myosotis* dynamics.

Parameter B, the basis for the flood dependence of population dynamics, was < 1. Thus, increasing flood duration gave decreasing transition rates for *Myosotis* abundance values and thus a negative impact of flooding. But multiplied with the flood-independent rate component A we had positive rates AB^{τ} for all τ-values with $\tau < 15$, i.e. over the whole range of flood duration. Hence, abundance values in the model would increase in all segments under all flooding conditions, and flooding would only slow down this abundance increase. But at the lakeside part

226 of the transect "catastrophic" flooding, expressed by eq. 8, could occur: from time to time,
227 *Myosotis* abundances broke down in the model, as was observed in the field (Peintinger, 2007).
228 Due to these events the model was able to reproduce population increase and breakdown as
229 observed in segments 3 and 4, i.e. in the segments with high flood impact.
230 From segment 5 towards the landside such catastrophic events never occurred. But in this range
231 *Agrostis* was present as a competitor with steadily increasing impact. From segment 8 upwards
232 *Myosotis* did not occur after the mid of the 1990s years.
233 These opposing forces, flooding catastrophes and competition, were responsible in their
234 interaction for the peak in *Myosotis* abundance, for the shift of this maximum in the years about
235 1990 and for its position, since 1995, in segments 4 to 6. These features were well reproduced by
236 the simulation model. However, our deterministic Markov model could not reflect the high
237 variability in abundance values as demonstrated by Fig. 3, where relative abundance changes
238 $R_i(t)$ (eq. 1) are plotted as functions of flood duration $\tau_i(t)$. In these plots, the *R*-values for both
239 field data and simulations decreased with increasing flood duration τ, with regression coefficients
240 of $b = -0.216$ and $b = -0.056$ (both significant at $p < 0.001$), respectively. Flood impact on
241 abundance changes was smaller in the simulation model than for the field data.
242
243 *Projections of future development*
244
245 The overall abundance of *Myosotis* increased between 1983 and 2009 but the linear regression
246 was not significant (Fig. 4A, $b = 13.6 \pm 33$). Simulated values (Fig. 4B) gave a significant
247 regression slope of $b = 49.2 \pm 13$. This increase may be overestimated as the 1991 "outlier" in
248 the field data could not be reproduced by the model. The positive trend in *Myosotis* abundance
249 was due to the slight decrease in average flood duration. Fig. 4B also demonstrates the damping

effect of *Agrostis* on abundance development by comparison with a "no-competitor" situation where *Myosotis* would have reached unrealistically high abundance values after only a few years. Long-term simulations gave unchanged average positions of *Myosotis* and *Agrostis* at the end of the projection period of 75 years (Fig. 5B). This projection did not take into account any actual trends in flood duration, as τ-values were drawn at random from the whole set of values of Fig. 1A. The calculated extinction probability denotes some risk for the species. A prolongation of average flooding period (Fig. 5A) led to a strong increase in extinction risk. The abundance peak shifted towards the landside, but the reduction of competitive stress by *Agrostis* could not balance out the increase in flood stress as there was a higher proportion of "catastrophic" flooding events. Reduction of average flood duration by 2 time units (1 month) supported *Myosotis* as the species was less affected by catastrophes (Fig. 5C). But a larger decrease in average flooding led again to a higher extinction risk, as space for *Myosotis* to escape *Agrostis* was limited towards the lake (results not shown). In Fig. 5D the consequences are shown of a reduction of average flood duration accompanied by a larger spread of values, with "catastrophes" occurring in almost the same proportion as before. Here, *Myosotis* was limited by the lake, by the competitor *Agrostis*, and threatened by extreme flooding: extinction risk was again increasing as compared to the present situation.

Discussion

Population dynamics and Markov modelling

We demonstrated that a Markov simulation model, combined with regression analysis, is able to handle long-term spatially resolved species monitoring data, even with gaps in the time series,

and that it allows to consider environmental factors explicitly. For *Myosotis rehsteineri* the results supported the general hypothesis that along a water-depth gradient species distribution of littoral plants is restricted by flood tolerance at the lakeside and competition at the landside (Blom & Voesenek, 1996). On the basis of these two mechanisms our model was not only able to reproduce trends in total abundance but also spatial patterns and zonation along the water depth gradient. It reproduced the shift of maximum abundance to lakeside segments (Fig. 2B) and the strong abundance increase at 360 cm from 2004 onwards. It did not give the transient maximum at 360 cm in 1991, but here data are missing that would indicate abundance development in the years immediately before 1991. Besides this, it did not fully reproduce the observed stochasticity in abundance values. The neglecting of demographic stochasticity was of minor influence at abundance values of $10^2 \ldots 10^3$. But we must also assume a multitude of unknown stochastic elements (e.g., temperature, soil properties, recruitment from a seed bank), and it is a common situation in ecological modelling that only a quite small part of data variability can be explained (Clark 2007).

The high among-year variability of *Myosotis* abundance confirms the results of earlier shorter-term studies (von Brackel 2001; Grabher, Loacker & Aschauer 2006; Peintinger 2007). The abundance of *Myosotis* decreased after long floods, and the effect was stronger than that on the species *Littorella uniflora* and *Ranunculus reptans* (Peintinger et al., 2007). Evidently, these co-occurring species are physiologically and morphologically more adapted to flooding than *Myosotis*. Also limited gas exchange, algal shading and mechanical disturbance by wave movements may be important factors explaining the high mortality of *Myosotis* after long floods (Sand-Jensen & Borum 1984; Keddy 1984).

Although plant zonation patterns and water-level fluctuations are central issues in wetland ecology (Keddy 2010), only few studies investigated the population dynamics of amphibious

298 plants in the longer term (Szmeja 1994a, b). Except for studies at Lake Constance we are not
299 aware of any comparable long-term investigations at other sites of population dynamics of
300 lakeshore plants in relation to water-level fluctuations.
301 Neglecting the competition term of eq. 7 in the model (Fig. 4B) led to an exponential increase in
302 *Myosotis* abundance over a large part of the transect. Hence, competition is an important factor in
303 areas with low flood impact, and we assumed that it is mainly exerted by *Agrostis*, which is the
304 most abundant grass species in this lakeshore community. It forms dense turfs and can overgrow
305 the rather small plants of *Myosotis*. The abundance of *Agrostis* and, therefore, the intensity of
306 competition is increasing with elevation. Both species suffer during extreme long-standing
307 floods, but *Myosotis* is less sensitive and is faster to re-colonize the vegetation-free parts of the
308 lakeshore during periods of low flood duration, as shown by the strong increase to about 5000
309 inflorescences in 1991 and 2007. Thus, a coexistence of *Myosotis* and *Agrostis* can be maintained
310 over the transect by spatial segregation: the dominating *Agrostis* grass is limited in its spread by
311 regular flooding, leaving a zone where *Myosotis* can both escape the competitive stress by
312 *Agrostis* and sustain flooding, and only extreme flooding events are acting as "catastrophes".
313 Without annual water-level fluctuations *Myosotis*, constricted between flooding catastrophes and
314 *Agrostis* competition, would rapidly go extinct.
315
316 *Projection of species development*
317
318 Environmental variability is seen as a serious threat increasing the extinction probability at least
319 in small populations (Soulé 1987). But the studied population showed no decreasing trend in the
320 abundance data, expressed by the number of inflorescences, and the model simulations even gave
321 a slight increase within the study period. Hence, the population does not seem to be seriously

endangered under the present conditions. But the hydrology of Lake Constance, which is decisive for the maintenance of *Myosotis*, is expected to be affected by climatic changes in the next decades (Ostendorp et al. 2007). Following our model already an increase of average flooding duration by 1 month will markedly increase the present extinction risk. A reduction of average flood duration, as was observed for the last 25 years, will support *Myosotis* as long as it is small (less than 1 month). Such small changes, a rather probable scenario, will increase the viability of the species. But a still stronger reduction will heavily increase the danger of extinction. This scenario seems quite unrealistic as long as the water regime will not be regulated. But one must expect a higher variability of flood duration: also with a general decrease in flood duration, extreme values must be expected which again increase the extinction risk (Fig. 5D). There are incalculable features: we generally underestimated the effect of short-term abundance fluctuations and also the fact that the transect population was embedded into a much larger one. Nevertheless, the extinction projections indicate that changes in the present flooding regime will negatively affect our target species.

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Appendix: Supplementary material

345 The online version of this article contains additional supplementary text and data. Please visit
346 Appendix A.
347
348 **References**
349

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Legends to figures

Fig. 1. Flood duration and transect profile. (A) Flood duration τ_0 (in time units of 15 days) at the level of 340 cm (corresponding to transect segment 3) from 1960 to 2008 and regression line (slope b = -0.042 + 0.0295; p = 0.16 n.s.). (B) Elevation h (in cm) of transect segments i and corresponding flood duration. Flood duration τ (in time units of 15 days) was calculated by $\tau = \tau_0 - 0.076\ (h - 340)$, with $\tau_0 = 9$ as an example.

Fig. 2. Field data (number of flowering rosettes per transect segment) and corresponding simulation values from non-linear regression from the two-species Markov model for *Myosotis rehsteineri* and *Agrostis stolonifera*. – (A) *M. rehsteineri* abundance values from field records 1983-2009 and (B) from the simulation model with parameters of Table 1. (C) Frequency values for *A. stolonifera* from simulation with parameters of Table 1.

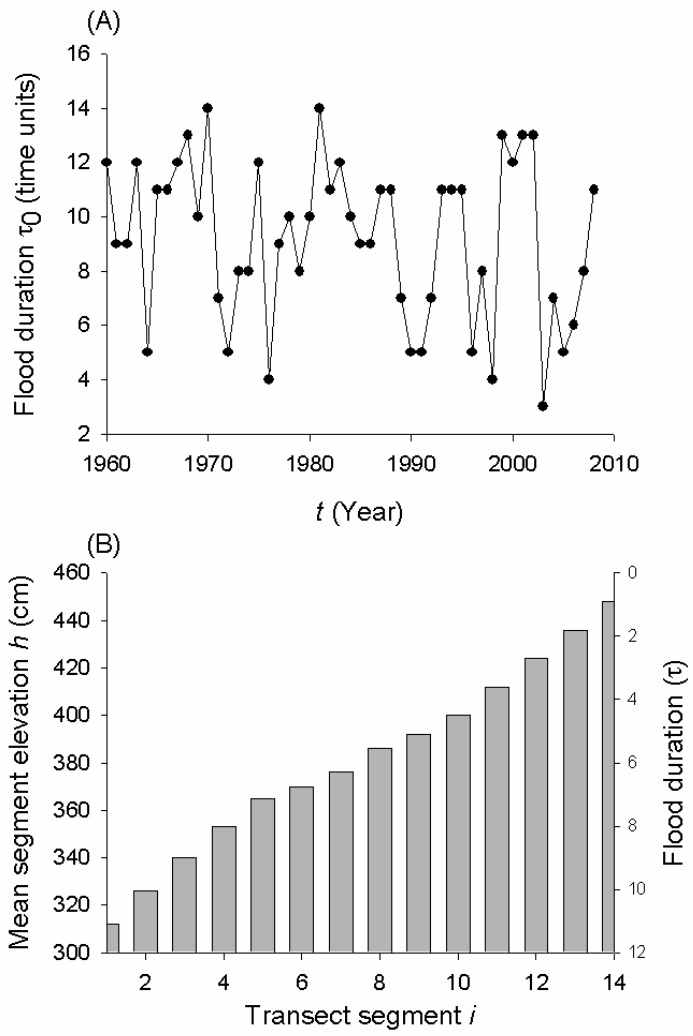
Fig. 3. Relative abundance changes $R_i(t) = \ln[(a_i(t)+1)/(a_i(t\text{-}1)+1]$ of *Myosotis rehsteineri* for year *t* and segment *i* plotted against the corresponding flood duration in year *t*-1. The segments are denoted by symbols and shades of grey. The presentation of empirical values only considers pairs of abundances a_t and a_{t-1} where both values were registered in the field. – Regression coefficients: (A) $b = -0.216 \pm 0.06$, (B) $b = -0.056 \pm 0.01$; both values significant at $p < 0.01$.

Fig. 4. Abundance values for *Myosotis rehsteineri*, summed up over the whole transect, in the study period 1983-2009, and general trends. (A) Field data; regression coefficient $b = 13.6 \pm 33$ (n.s.), (B) Simulation values; regression coefficient $b = 49.2 \pm 13$ ($p = 0.008$). – The open symbols in (B) denote abundance values simulated without competition by *Agrostis stolonifera*; the values for 1987 onwards are not shown (> 50,000 inflorescences in 2009).

Fig. 5. Final segment distribution profiles for *Myosotis rehsteineri* and *Agrostis stolonifera* and extinction probabilities for *Myosotis rehsteineri* after simulation over 75 years (average values per segment; 1,000 simulation runs). Flood duration values τ were drawn at random from the set of values given in Fig. 1A, modified by addition of $\Delta\tau$ with $\Delta\tau = +2$ (A), 0 (B) or -2 (C and D). In (D) the highest τ-values ($\tau = 14$) remained unchanged.

Table 1. Parameter estimates for the two-species Markov model (eqs. 6 and 10) for *Myosotis rehsteineri* and *Agrostis stolonifer*a. The parameter list for *A. stolonifera* includes values (a) from Peintinger et al. 2007) (averages over two transects of this study). – Standard deviation of the regression curve: *s.d.* = 230.

Species	Parameter	Value	Comment
M. rehsteineri	A	2.11 ± 0.22	Flood-independent growth
	B	0.951 ± 0.016	Flood-dependent growth
	d	0.0011 ± 0.0005	General dispersal
	D	0.020 ± 0.0075	Neighbourhood dispersal
A. stolonifera	A_{AS}	1.85	Flood-independent growth (a)
	B_{AS}	0.92	Flood-dependent growth (a)
	D_{AS}	0.0906 ± 0.066	Neighbourhood dispersal
Interaction term	γ	0.60 ± 0.07	see eq. 8



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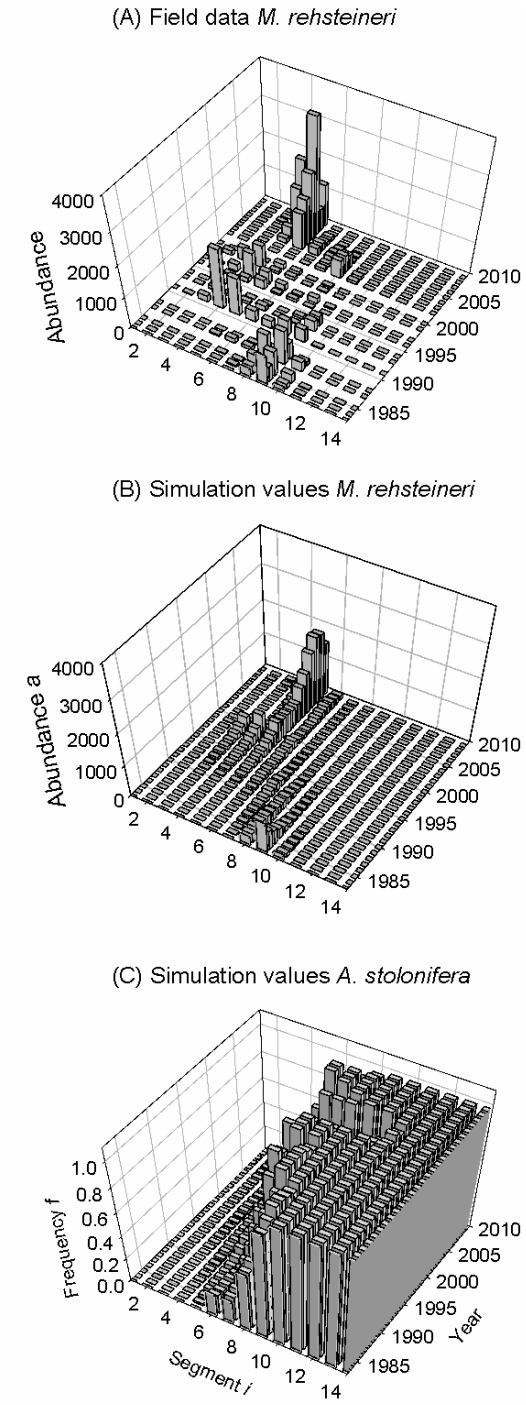
451 Fig. 1



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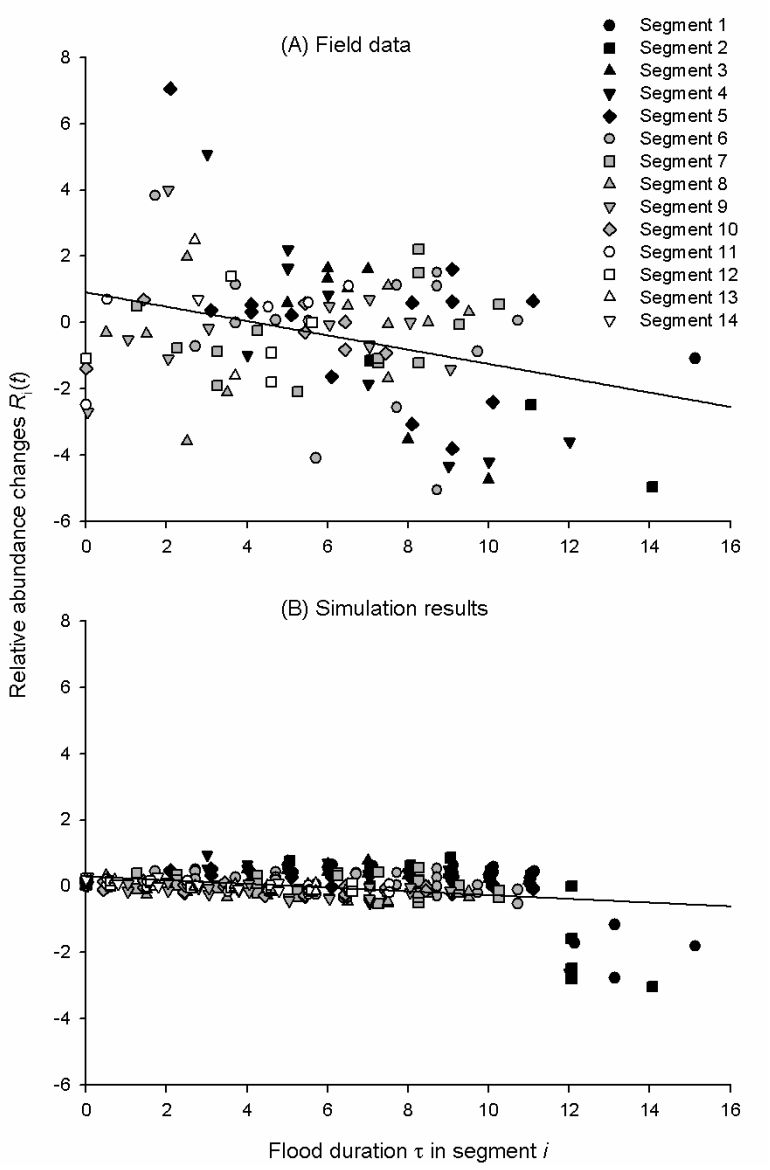
454 Fig. 2



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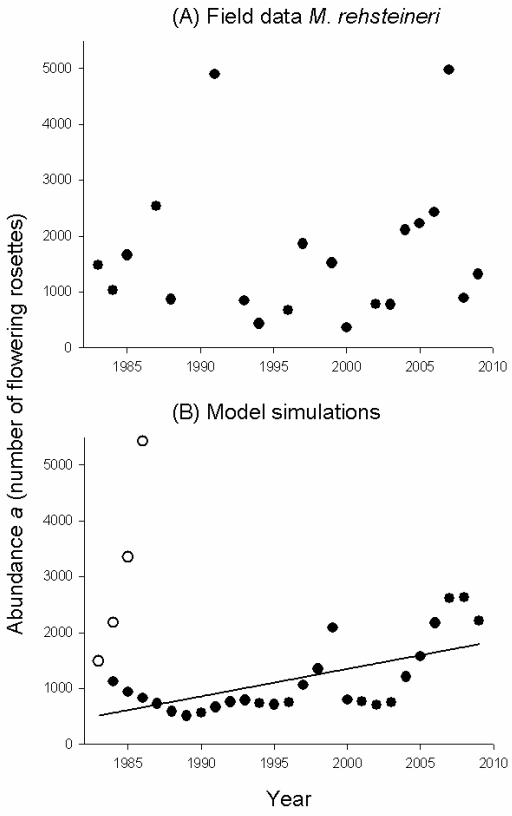
457 Fig. 3



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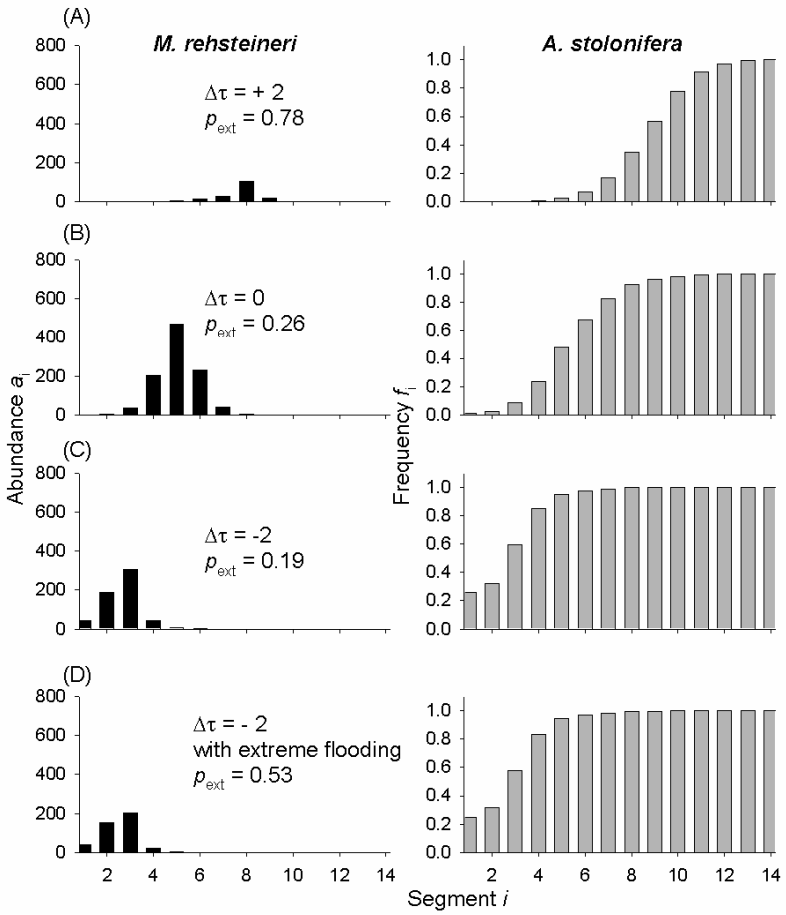

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463 Fig. 5